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PAIRING BEHAVIOR IN *HODOTERMES MOSSAMBICUS* (ISOPTERA)¹

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INTRODUCTION

The dispersal flight of termites, especially of those species living in savannah areas with alternating dry and wet seasons, is generally related to the beginning of a rainy period. The precise time of flight may be controlled by exogenous or endogenous factors and varies from species to species. Most species fly at dawn or dusk or at night whereas the few daylight-fliers usually swarm only under humid atmospheric conditions. After individual landing the alates of both sexes will meet in pairs. A typical "calling" posture of the female was observed in many species and was interpreted by several authors as chemical attraction. However, no precise evidence for this interpretation was given from field observations and no data about the spatial range of attraction were specified. After meeting, the sexes of many species proceed in "tandem", a typical formation, in which the male usually follows the female closely on the search for a suitable nesting site. The termite considered herein, *Hodotermes mossambicus*, is a dry grass harvesting species, exceptionally adapted to survive under extreme climatic conditions of semi-arid grasslands. The species differs in several aspects from other termites: the workers forage in relatively loose formation above ground often in sunshine and are able to use individual op-

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tical orientation in contrast to the usual feature of foraging columns confined under galleries or in narrow pheromone trails (Leuthold *et al.*, 1976). In contrast to other termites, they have functional compound eyes and darkly pigmented body surface. Alate imagines and workers carry their own water supply in specialized water sacs, according to Watson *et al.* (1971). We had the opportunity to observe carefully the pairing behavior of *H. mossambicus* on a single swarming day (9.4.1976) in Olorgesailie, Kenya. This study revealed an unusual modification also in the pattern of pairing behavior. The reproductive dispersal flight occurs during the hot period in the afternoon, often during full sunshine on the day after a rainfall. The roles of male and female were found reversed relative to the behavior observed in other termites. A mechanism of pheromonal sex attraction was clearly concluded from the behavior. Unfortunately, another flight during which we expected to carry out planned experimental analysis did not occur during our available observation time.

OBSERVATIONS

The climate of Olorgesailie, the area of observation in the great Rift Valley near Nairobi, is characterized by extensive dry periods and sporadic rainfall of 300–400 mm per year, concentrated in the months of February to May and to a lesser extent from October to November. Swarming of *H. mossambicus* in this area takes place after substantial rainfall following the main dry season (recorded data of rainfall that released flight: 1.3 mm, 35 mm and 21.2 mm). In this area the swarming often extends over several rains if the showers are only weak and sporadic. Swarming was recorded on (23.12.1971), 8.1.1973, 25.2.1973, (20.2.1974), 9.4.1976 and 3.4.1977.³ The time of swarming recorded was always in the afternoon under sunny conditions on the day following rainfall. One expected flight did not occur with overcast sky and slight drizzle.⁴

³Partly recorded by Mr. Kannugi, warden at the prehistoric site in Olorgesailie. The figures in parentheses are not well documented.

⁴Hewitt and Nel (1969) reported flight after a latency time of 4 to 6 days after the first substantial summer rains, in the Orange Free State in South Africa. They did not mention the meteorological conditions before and during flight. It seems worthwhile to collect more data in both areas to decide whether the populations in the two zones of very different latitude (1.6°S and 29°S) behave differently in this respect.

The swarming referred to in this paper occurred on 9.4.1976 around 16.30 h (sunshine). After a short dispersal flight of less than 100 m the alates landed individually on the ground, shed their wings and started running about. [Behavioral details of this sequence have been described by Hewitt and Nel, 1969.] The MALES rambled with their abdomens raised in "calling" position and their huge sternal glands exposed (Fig. 1) in search of a digging ground. If they found a suitable place, they started excavating a hole by flicking dust particles out with their legs and often carrying out soil bits with their mandibles. They held their abdomens permanently in "calling" posture as long as they were unpaired. The unpaired FEMALES, on the other hand, repeatedly climbed on elevated structures, such as grass stems, apparently for "sniffing" for the male's scent. They clearly perceived the presence of a male from a distance of at least 2.5 m up-wind. They obviously became excited and ran slightly zig-zag towards the calling male, without ever failing to reach the goal (Fig. 2). The joining of a female with a digging male was analyzed from two film sequences: the female touched the male's abdomen with her antennae. On this stimulus the male turned around through 180° and palpated the female's abdomen intensively. With that stimulus, apparently, the male terminated calling behavior by lowering the abdomen and retracting the sternal gland. Henceforth, no other female was attracted, not even from as close as a few cm. The pair met either during the male's exploratory run or on the male's digging site. In the latter case the female participated in excavating behavior. In the first case she followed him in loose formation on the search for digging terrain. However, no rigid pattern such as that referred to as "tandem run" was ever observed. In suitable ground the digging pair disappeared from the surface within minutes. If the substrate was too hard or if the pair was attacked by ants, the male went on in search of another place, followed by the female. In the postflight behavior the male was always the attracting and leading partner and the female actively hunted for him. If the female was experimentally removed from the pair, the male resumed calling behavior. However, reproductives collected in petridishes did not resume sex attraction behavior when separated and tested the day after flight in the laboratory nor did a crushed male sternal gland under those conditions attract any female.



Figure 1. *Hodoterpes mossambicus*: dealate male in "calling" posture and at the same time excavating a hole. The zone of the sternal gland is widely protruded (light area marked with arrow).

AIRBORNE PHEROMONAL ATTRACTION

A female motivated for pairing is clearly attracted from a distance apparently by a volatile chemical stimulus from the male. When the female crossed a zone 250 cm or less down-wind from the male, an immediate reaction of intensified excitement and orientation towards the male was always observed. [Eleven observations on the natural ground were recorded in which some females were used for a second run after experimental displacement. Reactions over distances up to 3 m or even more seemed to be possible but have not been systematically recorded. The wind was a light breeze, windspeed in one case determined roughly 1.5 m/sec.] The possibility that visual cues from the male could be responsible for the accurate female orientation was clearly disproved, since the same pattern of orientation was observed when the male was not visible to the female. Another argument for pheromone mediated orientation is the strong correlation of sex attraction response with the exposure of the male sternal gland. When this was retracted (after a female had joined the male) another searching female was no longer attracted, even if the male was visible. Females within the active space of attractive pheromone approached the goal in a fast agitated run (5 to 10 cm/sec) performing a characteristic orienting pattern (Fig. 2). The female's body-axis altered its direction in short irregular turns, performing an irregular broken zig-zag line. In superimposed movement the insect walked a greater waveline or zig-zag along the main axis leading to the source. A female in up-wind position relative to the male oriented positively only at distances closer than 6 to 10 cm. This was observed under natural conditions and after experimental displacements of the female. The observed overall pattern of orientation (Fig. 2) is principally compatible with the theoretical model of airborne chemical orientation as reviewed and discussed by Farkas and Shorey (1974). This postulates, first, motivation of the insect by the chemical stimulus to anemotactic orientation, i.e. steering in general up-wind direction. Secondly, the course is finely adjusted by a mechanism of orientation (e.g. osmoklinotaxis, osmotropotaxis or a combination) that involves correction of the lateral deviation from the central axis of the aerial trail and enables the insect to remain within the odor plume. At close range, where the gradient of concentration

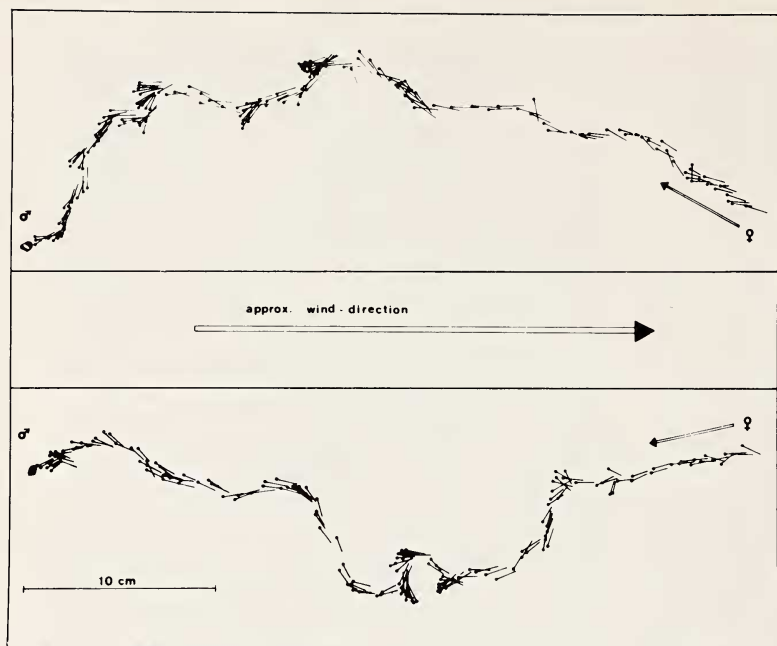


Figure 2. Two walking patterns of females orienting up-wind towards the "calling" male, redrawn in sequence of 1/18 sec from ciné film. The small dots represent the position of the female's head, the tails indicate the body axes. The wind was a light breeze of unknown speed, the direction was approximately determined with cigarette smoke.

is assumed to be steep, direct osmochemotactic orientation is postulated without the need of air movement. An experimentally proved analysis of the postulated mechanisms has not been firmly worked out so far, and neither can the answer be given for the case of *Hodotermes* sex attraction. This species, however, appears to be an ideal subject for experimental analysis because of the insistent motivational impetus in the performance of postflight behavior except for the difficulty in catching the swarming time.

The Sternal Gland

The sternal gland in termites is known as the source of the trail pheromone (Stuart, 1969 and 1976; Bruinsma *et al.*, in prep.). The involvement of the gland in sexual attraction during the imagines'

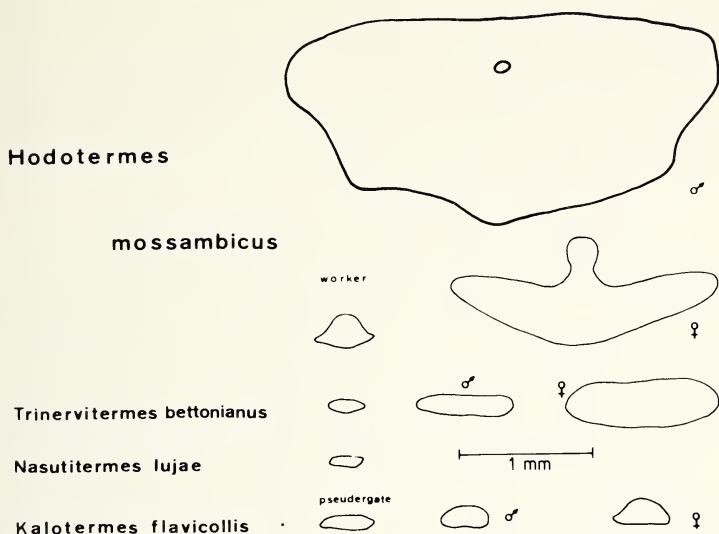


Figure 3. Comparative sizes of termite sternal glands: the contours of the glands in top view of *H. mossambicus*, reproductive male and female (after flight) and major worker; those of *T. bettonianus*, characterized by Leuthold and Lüscher (1974) as unusually hypertrophic in the reproductive caste; those of other species [*N. lujae* after Pasteels (1965), *K. flavicollis* from own drawings]. The glands were drawn from fresh whole-mount preparations in Ringer solution.

postflight behavior had been assumed from calling behavior by several authors (reviewed by Stuart, 1969). A few species have been more closely analyzed: In *Kaloterme flavicollis* (Kalotermitidae) calling females have been only occasionally observed with exposed sternal glands (Wall, 1969). A more intensive relationship of the sexes was found in the tandem behavior in which either the male or the female could be leader. Both sternal and tergal glands were experimentally verified as sources of sex attraction from laboratory bioassays. The sternal gland of the female was exclusively male attractive. The male tergal gland was dominantly attractive to females and to a lesser extent to males, and the female tergal gland was slightly active towards both sexes (Wall, 1971). Pasteels (1972) reported calling courtship but no distinct tandem pattern in *Zootermopsis nevadensis* (Hodotermitidae). In most cases the female was the calling partner but apparently for the first time also

a male was seen calling. Extracts of sternal glands released reciprocal attraction between the sexes. The glandular secretions of imagines were found to be sex specific and different from the trail pheromone of the nymphs. *Reticulitermes flavipes* (Rhinotermitidae) performs distinct female calling courtship and tandem behavior with the female leading (Buchli, 1960). Reciprocal attraction of extracted sternal glands was found between males and females (Stuart, 1975). In *Trinervitermes bettonianus* (Termitidae) the attracting and leading partner is always the female, as it usually is for the family. The calling female exposes both tergal and sternal glands (Leuthold, 1975). The former attracts on longer range distances, up to 12 cm; the latter on short distances, up to 1.5 cm in the laboratory. Both glands are involved in holding the tandem connection, but the sternal gland is more important in this function (Leuthold, to be published). Furthermore a powerful trail is deposited during tandem run. The imaginal sternal gland pheromone may not be different from the worker trail pheromone (Quennedey and Leuthold, 1977). The relative volume of the female gland, however, is unusual and reaches 7 times that of the male and 65 times that of the worker gland (Fig. 3), and trail activity was found to be 1200 times as high as that of a worker gland (Leuthold and Lüscher, 1974).

The sternal gland of *Hodotermes* (Hodotermitidae) is the largest termite sternal gland ever reported (comparative sizes in contours of various species are represented in Fig. 3). The morphology of the gland in *Hodotermes* is complex and it seems that different glandular structures are differently developed in the various castes [A study of morphology is in preparation by Quennedey and Leuthold]. Trail activity of the sternal gland of *Hodotermes* male was lower than that of the worker gland and not different from the control (male sternal plates without the gland). The extracts were tested in the bioassay described by Leuthold *et al.* (1976). The apparent function of the male gland is airborne female attraction. The pheromone produced is definitely different from the trail pheromone of the workers. [Unfortunately no attractant test in the field with isolated or extracted glands could be carried out during the single swarming event available.] As mentioned above, the attracting and leading partner in courtship was always the male as far as we have observed. However, Hewitt and Nel (1969) apparently have seen both sexes calling in the same species in the Orange Free State

in South Africa. This would bring light to the question of the unknown function of the female sternal gland, which is obviously different in shape from that of workers and reproductive males (Fig. 3) and yields the same trail-activity as a worker gland when extracted and tested in the standard trail-bioassay.

DISCUSSION

Dispersal flight in *Hodotermes mossambicus* was observed during full afternoon sunshine on open land. This is a rather exceptional behavior in termites (Nutting, 1969) and comprises considerable hazards of desiccation and predation. How do the alates prevent desiccation? According to Watson *et al.* (1971) the imagines have specialized water sacs (salivary reservoirs) which they fill after flight by active water uptake (in the laboratory). The authors did not say whether or not water is carried along during the flight. This would seem useful, in our opinion, to compensate for water loss during flight and post-flight behavior and for the initial development of the colony in case no other rain falls after swarming. As mentioned above, a low rainfall of only 1.3 mm may trigger flight for the following day. This may occasionally be the only rain for a longer period of time. On the day of flight the soil surface is still slightly humid but probably not sufficiently so for the insects to imbibe free water. Therefore, it would be interesting to investigate the question of water storage in the hot semi-arid zones of Kenya. The hazard of predation on open land on sunny afternoons is considerable. Birds are extremely active and are efficient predators during the time of swarming. We have furthermore observed significant predation by lizards, ants, and salticid spiders. However, a good percentage of all the swarmed imagines escapes predation thanks to the very efficient system of pairing. *Hodotermes mossambicus* together with two other hodotermitid species (*Anacanthotermes* sp: Clément, 1956) are, to my knowledge, the only observed species where the attracting partner is already digging while still single. *Hodotermes mossambicus* represents the only documented case in termites of airborne chemical sex attraction on long distance. In most observed cases pairing took place efficiently within seconds or a few minutes from alighting. If pairing was not successful by the time the male's excavation had reached the depth to enable him to disappear underground, he stopped digging or started another hole. However, we did not observe such a case except when the ap-

proaching females were experimentally removed. The question arises: why does *Hodotermes* fly during the time of highest predation and desiccation and not, like many other species, under damp and rather dark conditions during or soon after rain? Some aspects of adaptation to the extreme habitat are considered: in the arid areas the dry soil is often dusty and does not absorb the water rapidly. The rains often are short, heavy thunderstorms. After a first rain-shower the soil is generally flooded or muddy and swarming during or shortly after the rain would be fatal. Waiting for a repeated rainfall, when the soil is wet enough to absorb, as do certain other termites (e.g. *Trinervitermes bettonianus*), could possibly mean waiting forever, since rainshowers may be very sporadic. The day after rain the soil is still humid, and if the sky is clear in the afternoon there is little risk for another flood immediately after the flight. Such a situation may be interpreted as a suitable flying condition from this point of view. It is worth mentioning that the species generally is obviously challenged to sunlight, as revealed also in the workers' pigmentation, their developed compound eyes and sunlight orientation.

SUMMARY

Swarming in *Hodotermes mossambicus* was always observed at the beginning of a rainy period in afternoons during sunshine, the day after a first rain.

The dealate male exposes his sternal gland for airborne female attraction ("calling") (Fig. 1). The male sternal gland is the largest ever found in termites (Fig. 3). The male begins with excavating into the soil while calling. The female (running about) is stimulated by the male pheromone from 250 cm up-wind and orients in a winding zig-zag run towards the calling male (Fig. 2). After they join, the male stops "calling" and the female takes part in digging. The behavior of "tandem run" was not observed. The pair disappears within minutes from the surface.

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